Photo 1: Male of the Animba population of Poropanchax scheeli. Photo: M. Chauche.

Photo 2: Female of the Animba population of Poropanchax scheeli. Photo: M. Chauche.

The Estuarian Cyprinodont Angel

Poropanchax scheeli (Roman, 1970)

(Aplocheilichthyinae, Cyprinodontiformes): Its First Discovery From Gabon, With Further Insights On African Lampeyes Systematics And On Specialized Cyprinodonts Distribution In Brackish Waters.

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Abstract:

A lampeye with angel fins, *Poropanchax scheeli*, dwelling brackish estuaries, is reported for the first time from Gabon. The distribution is then extended by about 230 kms to the South. Its ecology, behavior and aquarium maintenance are described: it is hypothesized that breeding, growth of fry, up to the subadult stage, occur in black soft waters, whereas adults may shoal in larger brackish waters. The evidence of pores and tubular channels on front of adults, to the contrary to Northern populations, pushes to confirm its systematic placement in the recently rediagnosed (Huber, 1998a) genus *Poropanchax*. And, to hypothesize a link with the taxon *Congopanchax*, its subgenus, via a bridge in their disjunct distribution materialized by the lower Congo River. Finally, further biogeographical considerations are forwarded about the specialized oviparous Cyprinodonts which dwell brackish waters on vast ranges.

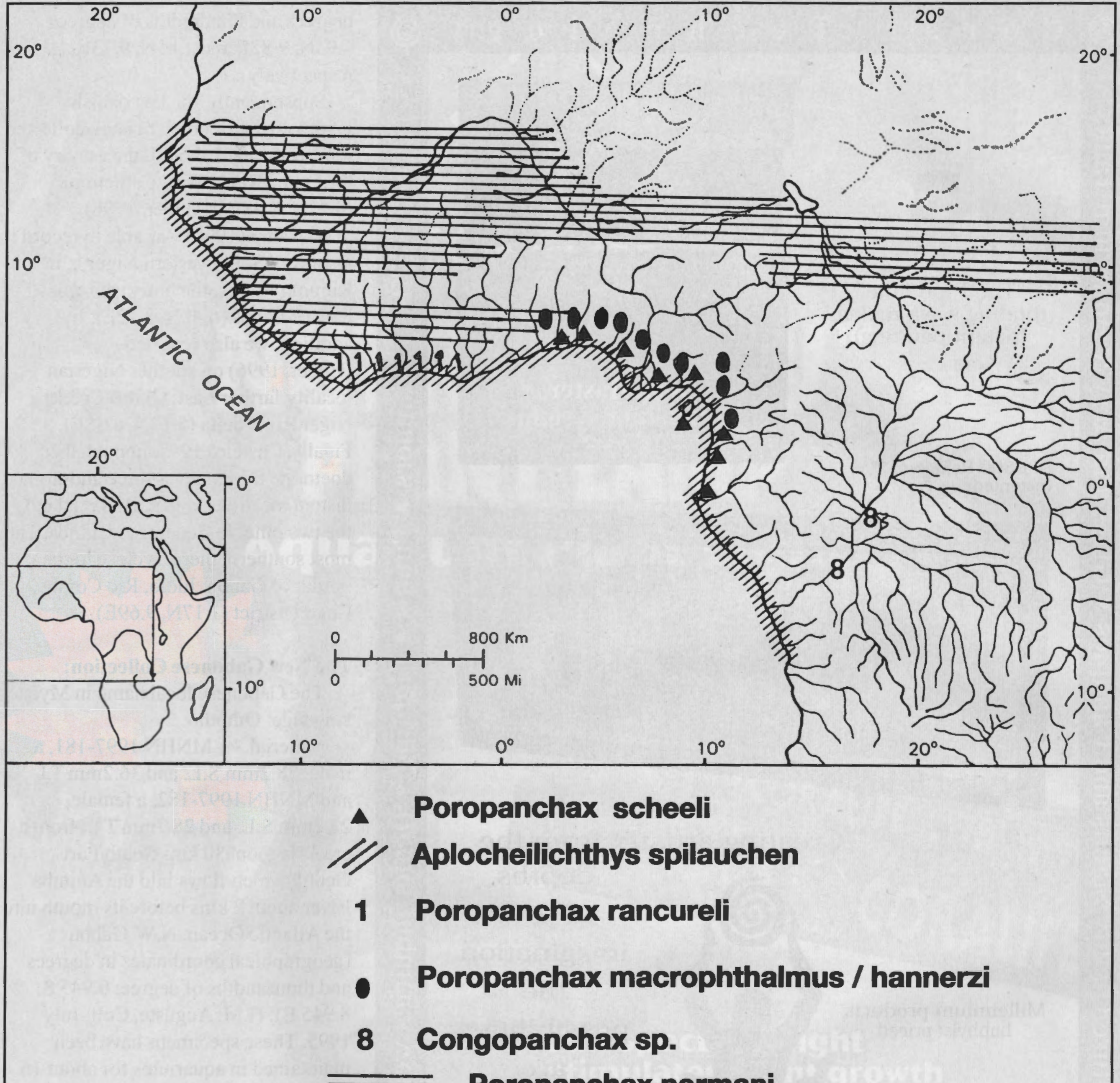
Résumé:

Un "Oeil-brillant" aux nageoires filamenteuses, *Poropanchax scheeli*, habitant les eaux saumâtres des estuaires, est rapporté pour la première fois du Gabon. Sa distribution est ainsi étendue d'environ 230 kms vers le Sud. Son écologie, son comportement et sa maintenance en aquarium sont décrits: l'hypothèse est proposée que la reproduction, la croissance des jeunes jusqu'au stade subadulte, ont lieu dans les eaux douces "noires", tandis que les adultes vivent en bancs dans des plans d'eau saumâtre plus importants. La mise en évidence de pores et de canaux tubulaires sur le front des adultes, au contraire des populations septentrionales, conduit à confirmer son positionnement systématique dans le genre *Poropanchax*, tel que récemment diagnostiqué (Huber, 1998a) et à suggérer un lien avec le taxon *Congopanchax*, considéré comme son sous-genre, via un pont dans leur distribution disjointe, matérialisé par le bas Congo. Enfin, de nouvelles considérations biogéographiques sur les Cyprinodontes ovipares spécialisés habitant les eaux saumâtres avec de vastes aires de répartitions sont proposées.

Surprise after surprise, Gabon, a small country of Western Africa is becoming one of the richest of all in terms of density of species over the whole distribution of Cyprinodonts.

In Killi-Data 1996 (Huber, 1996), we have reported on 49 species from Gabon, with 31 *Aphyosemion* sp., four

Photos 3, 4, 5: Different views of the biotope of the Gabonese estuarian Angel. Photos: H.M. Auguste.



Map 1. The present distribution of Poropanchax scheeli and related Aplocheilichthyins. Original drawing by R.H. Wildekamp, modified by the author.

Diapteron sp., six *Epiplatys* sp., one *Aplocheilichthys* sp., two *Hypsopanchax* sp., one *Hylopanchax* sp., five *Procatopus* sp. (subgenus *Plataplochilus*). Since then, four further enthusiastic killi-hobbyist expeditions, two from California another from Germany, and the last from Switzerland, have taken place. They allowed to add 2 new species of *Aphyosemion* (*A. hera, A. tirbaki* n.sp.), plus the new records of *Aphyosemion buytaerti*, *A. schluppi*, and *Diapteron seegersi*, previously known only from neighboring regions of Congo.

Today, we register one additional species, *Poropanchax scheeli*, discovered by Henri Michel Auguste, a local Gabonese aquarist living in Port Gentil, while searching for a suspected counterpart of *Poropanchax macrophthalmus* in his home surroundings.

The species has been collected from the Animba River, i.e., some 230 km south of the Southern-most collection of the species in Equatorial Guinea.

The total number of Gabonese Cyprinodont species amounts now to 55 over 268,000 square kilometers, i.e., a density of 0.2052 per thousand square kilometer (countries with richer fauna are much bigger: Brasil, 92 species, USA, 77 species, Cameroun, 68 species, in Huber, 1996). And, this amount is still underestimated because a very important region, the North of the Massif Du Chaillu is still unprospected.

Actually, Gabon combines all known ecobiogeographical criteria which enhance speciation in Cyprinodonts: a present equatorial position, a sharp contrast between the coastal plain and the inland plateau, a hilly landscape building exchange-proof compartments, a dense primary forest with some limited derived savannas, a good variety of past climates with

refuge zones, and the nearby inland lowlands of the Congo basin, easterly to serve as an additional pressure of competitive fauna. Plus, the dead end ocean barrier with fluctuations in the level of the sea over history, which is of primary concern to us. Besides, the region South of Port Gentil is occupied by the Ogooué River delta, with lagoons of soft seasonal and brackish waters. Thus, we expected to record the same type of fauna as in the Niger delta in Nigeria or the Lobé and Kienké deltas in Cameroun or the Ekuko (Ecucu) delta in Equatorial Guinea, including, annual species related to *Aphyosemion*, namely in *Gularopanchax*.

***Poropanchax (Poropanchax) scheeli* (Roman, 1970)**

History of collections

This unique lampeye was discovered by the late Spanish ichthyologist Benigno Roman, who published a full study of the fish fauna of Equatorial Guinea in 1971: the types have been collected in Rio Utonde and Rio Ekuko, near their mouths in August 1968 (geographical coordinates, in degrees and hundredths of degrees: 1.93N, 9.82E and 1.83N, 9.73E, respectively).

Subsequently, the late danish ichthyologist, Joergen Scheel, collected it in 1969 near Bikundi, the estuary of the Ombé River, West Cameroun (4.22N, 8.98E in Huber, 1996). Wildekamp (1990) was able to record it also from Southwestern Nigeria, in Kuramo waters, the brackish lagoon East of Lagos (6.40N, 3.42E). In addition, we also reported (Huber, 1996) on another Nigerian locality farther East: Okoso Creek, Niger River delta (5.13N, 6.38E). Finally, Castelo (1995: unpublished doctorate thesis) gives three additional distant localities, one in Bioko Island, the two other in Equatorial Guinea. The most southern, there, is close to the border of Gabon: Idolo, Rio Combe, Cogo District (1.17N, 9.69E)

The New Gabonese Collection:

The Gabonese local name in Myéné language: Othotho.

Material. — MNHN 1997-181, a male, 28.2mm S.L. and 36.2mm T.L., and MNHN 1997-182, a female, 22.2mm S.L. and 28.7mm T.L. from a creek-lagoon, 30 kms South Port Gentil, which flows into the Animba River about 2 kms before its mouth into the Atlantic Ocean, N.W. Gabon (geographical coordinates in degrees and thousandths of degree: 0.945 S, 8.945 E); H.M. Auguste, Coll. July 1995. These specimens have been maintained in aquariums for about 16 months before preservation. On collection, their total length was circa 13mm.

Morphomeristics of the two specimens, male first, both radiophotographed:

Total length (in % of S.L.): 128%, 129%.
Predorsal length (in % of S.L.): 68%, 67%.
Preanal length (in % of S.L.): 59%, 58%.
Preventral length (in % of S.L.): 39%, 42%.
Depth at Anal level (in % of S.L.): 23%, 18%.
Depth at Peduncle level (in % of S.L.): 15%, 10%.
Head length (in % of S.L.): 27%, 28%.
Interorbitar (in % of S.L.): 12%, 11%.

Eye diameter (in % of S.L.): 9%, 10%.
Snout (in % of S.L.): 6%, 5%.
Vertebrae (abdominal+caudal): 13+14, 13+15.
Dorsal fin rays: 6, 7.
Anal fin rays: 11, 11.
D/A deviation: +9, +8.
LL (scales in lateral series up to caudal peduncle, plus beyond): 26+2, 26+1.
Predorsal scales: 18, 17.
Transversal scales: 7, 7.
Circumpeduncular scales: 12, 13.

There seems to be a sexual dimorphism in fully adult specimens (kept over one year in an aquarium), in addition to fin length and shape: male is higher than female at the level of anal and of peduncle; however, this must be checked on more material.

The frontal scalation is of the G type. The scales on the sides are all hairy in both sexes, i.e., they show small filaments at their exposed edge.

The frontal sensory system is made of two exposed pores, linked beneath by a tubular channel. All external teeth are conical.

All fins are elongate in both sexes, but more in the male than in the female. Pectorals, ventrals, dorsal, and anal fins are acuminate in the male, rounded in the female. The dorsal and anal reach the level of the caudal peduncle in male.

Note that the ventrals are also elongate in the female, though less, to the contrary to Northern populations, where they are short (Wildekamp, 1995).

All the above data fit very well with Roman's, Castelo's, and Daget's observations: D: 6-8, A: 12-14, LL: 24-27 (Roman, 1971) in Equatorial Guinea; D: 6-7, A: 11-14 (mean: 13), V: 6, P: 9, LL: 25-28 (mean: 26) (Castelo, 1995) also in Equatorial Guinea; D: 7, A: 11-12 (Daget, 1979) in Cameroun. Castelo also gives detailed average morphometrics in percentage of S.L. Max. depth: 21.8% in male, 20.1% in female, head: 24.4% in male, 24.2% in female, depth at peduncle level in % of length of peduncle: 57% in male, 52.3% in female, length of dorsal fin in % of head: 89.2% in male, 67.8% in female, length of pectoral fins in % of head: 83.1% in male, 84.2% in female.

However, Wildekamp (1995) reports that the adults of the Nigerian populations, contrary to the Gabonese material, here, exhibit a non-tubular, but open supraorbital neuromast system. Then, he hesitates to place his material of *scheeli* in the taxon *Poropanchax* which was diagnosed by 3 supraorbital pores by Clausen (1967).

On the other hand, the specificity of the Gabonese material appears more complex than first evidenced. We have studied 20 specimens of a further collection from the same locality (MNHN 1998-483, collected on November 9, 1997 by H.M. Auguste) that were immediately preserved in the field and not grown in an aquarium. Surprisingly, the variability in the supraorbital neuromast structure was found to be very high.

On the 20 specimens, we counted only three cases with two pores on both the left and right sides of the front, two cases with two pores on one side and

Continued on page 61

Continued from page 56/52

three pores on the other, one case of three pores on both sides, two cases with pores on both sides and an intermediate narrow groove of interconnection, four cases with pores on one side and a groove on the other, eight cases of grooves on both sides, without pores.

This very high variability seems, though, to show a constant trend. Among the seven larger specimens (circa 20mm), pores are exhibited in 5 cases. Among the 13 smaller specimens (circa 10mm), nine cases of shallow grooves, at least on one side, are to be seen.

This complex situation justifies a deeper study of more material from the entire range for such a specialized, widely distributed species. However, it allows to propose the usage of *Poropanchax* with new diagnostic characters (see further, systematic relationships).

Diagnosis:

As properly stated by Roman (1971), *Porop. scheeli* is separated from all other lampeyes by its elongate and filamentous ventral fins, longer in males than in females. They nearly reach the level of the caudal peduncle in dominant males. It is not easily separable from the other components of the *Poropanchax* genus (*Porop. macrophthalmus*, *Porop. hannerzi*, *Porop. rancureli*, *Porop. normani* (?)) by further morphomeristic characteristics: the D/A deviation tend to be higher (D/A = +8 to +9 versus D/A = +6 to +8). However, its ecological niche is different (see ecology).

The fish had been named by Roman as a subspecies of *Porop. macrophthalmus*, but in 1971, he quotes Scheel: "with your material, I forward to you my material of the new subspecies (which undoubtedly is just as good a species as is rancureli and hannerzi)". The species status is given by Daget (1979), followed by Radda & Pürzl (1987), Wildekamp (1990, 1995) and also here, based on the derived characters of elongate ventrals, on the distribution, parallel and vicariant to *macrophthalmus et al.* and on the ecological niche. However, the french ichthyologist Romand (1992) and Castelo (1995) maintain conservatively the subspecies status. In-depth molecular studies are required, all the more that the frontal sensory system appears not to be diagnostic any more (see also Huber, 1981; 1998a).

Color pattern in life:

Male: the body background is yellowish, becoming whiter towards the belly. A brilliant blue shine, typical of lampeyes, irregularly covers the sides, more conspicuous posteriorly. A strong melanism is characterized by a thin black line at the border of each scale, plus dark dots in the middle of many scales; all fins are translucent yellow (Photo #1).

Female: subdued, with very little marking, except the "net" along scales. Fins are colorless (Photo #2). As usual in Aplocheilichthyins, both sexes have the distinctive reflective blue spot in the upper part of the iris (hence the lampeye name).

Color in preservative:

Very little is maintained from the life colors: a thin median dark line on the sides, as usual for all lampeyes, and a broader dark band on the basis of the lower sides. In the male, it goes from the anal insertion to the caudal peduncle.

In the female, it is even broader, but somewhat shorter. The typical dark "net," consisting of a line along each scale border, is less regular than usual, except above the median part of the sides. No pattern at all exists on the fins of both sexes.

Ecology (Photos #3, #4, #5):

"The habitat is a small shallow creek, with slow-moving waters during the dry season, somewhat less slow during the rainy season, which drains into Animba River. The junction between the creek and the coastal river is done through a marshy area with mangrove, aquatic and semi-aquatic plants (*Nymphea* sp., *Amania* sp., etc.) and trees characterizing flooded zones. A reversal of current, together with the rising of the water level, takes place with tide, because the Animba mouth with the ocean is just 2 kms away. Physico-chemical measurements of the water in July 1995: pH: 6.5, G.H.: 1.5,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K.H.: 0. On November 9, 1997, during low tide after a tropical rainfall, at 9:30 a.m. G.M.T., water temperature was 29.9°C, air temperature 31.0°C (before the rainfall, pH = 4.11). The water is black, because of the vegetal decay. The bottom is sandy and muddy. Peak high tides normally occur from June to the end of September or the beginning of October, within the dry season. Salinity is obviously varying quite a lot, every day, from low during low tide to much higher during high tide.

"In this spot, only young and subadults of *scheeli* have been captured and only during lowering tide. No adults were captured. The sympatric species are: two Cyprinodonts, *Aphyosemion australe, Epiplatys singa*, plus *Brycinus longipinnis, Hepsetus odoe*, a Cichlid (*Pelvicachromis taeniatus*?), and an unidentified pencil-like fish. The maximum observed life span of *scheeli* (fully adult fish with long filaments) seems over 16 months" (pers. comm. H.M. Auguste, November 12, 1996).

Actually, none of the quoted fishes can be collected during high tides of the rainy season: this suggests that all, including *Poropanchax,* swim upstream to avoid too high salinity contents. It is probable that, as in Nigeria, adults thrive in brackish lagoons, but not in seawater. Therefore, we hypothesize that parents are migrating into pure freshwater to breed. This hypothesis is in line with the fact that Cyprinodonts are secondary freshwater fishes (i.e., they must breed in soft waters, but do sustain a good proportion of salt in their biotope, which for some of them — *Cyprinodon dearborni, Rivulus marmoratus* — can even become hypersaline). Comparable, but not

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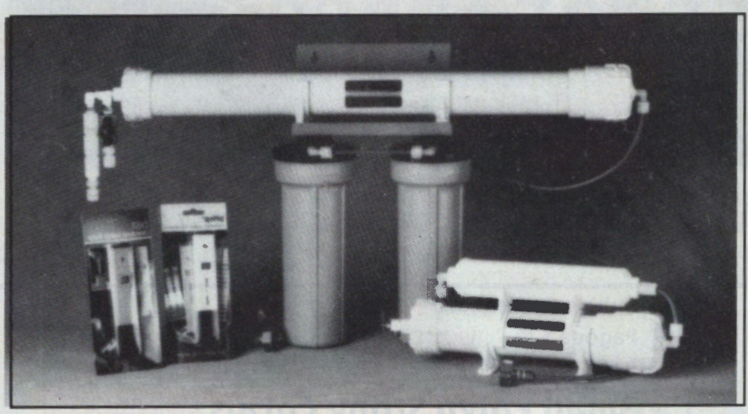

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identical examples are known for other Cyprinodonts like *Lucania* sp. which swim upstream of the coastal rivers of Eastern U.S.A. to find freshwater for spawning (but, see further the case of *Aplocheilichthys spilauchen*).

Behavior:

Porop. scheeli is a shoaling fish like all Aplocheilichthyins. It is not known if the dominant adults are often solitary, i.e., not compulsorily in groups, like the isolated lampeye *Aplocheilichthys spilauchen*.

Aquarium Experience:

The aquarium maintenance is difficult because of the requirements of a large tank (with a good length and some current, for this active swimmer), of a salty water (at least one teaspoon per gallon), and a planted environment. The light must be strong, from above, with floating coverage. The partial frequent water changes are primarily important (e.g., 20% each week).

This fish is strongly recommended to the experienced breeder. A shoal of several adults (up to 30) with their

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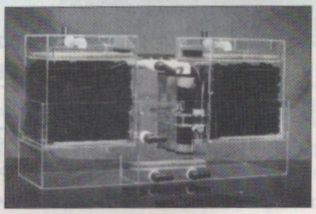

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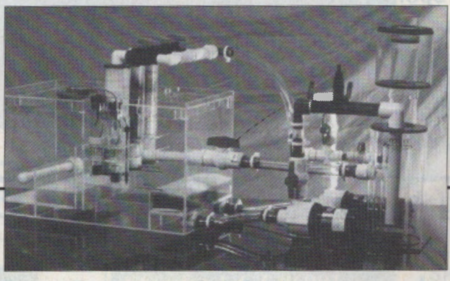

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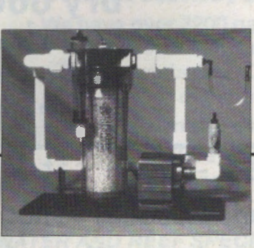

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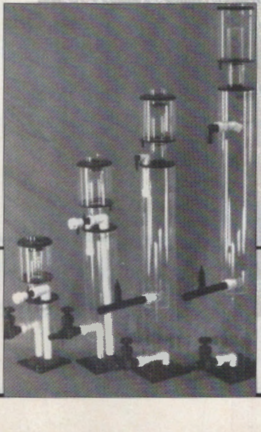

VENTURI PROTEIN SKIMMERS

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glazing-blue and reflecting colors, and their filamentous white fins, is a unique scene. The fish are very active and eat well (live food, exclusively; e.g., *Daphnia*, *Artemia salina*).

Spawning has been obtained occasionally with little prolificacy: eggs hatch after about 2 weeks' incubation in water. The fry is tiny and difficult to raise: food must be very small during the first weeks (small monocellular crustaceans and glassworms). Growth is very slow, maturity not being reached until 8 months and the adult size not before one year.

It is not known if the little prolificacy is attached to that species or if proper conditions are yet undisclosed. In that context, it is worth mentioning that we have witnessed the unexpected breeding of *Aply. spilauchen* in pure seawater, with excellent results in terms of progeny: a similar experiment should be attempted with *Porop. scheeli.*

Systematic relationships with insight into related Aplocheilichthyin groups:

In the original description, *scheeli* has been related by Roman to *macrophthalmus* on the basis of the morphology and fin shapes (acuminate with streamers in male, for the unpaired fins). However, *scheeli* seems to lack the separated longitudinal blue shining bands on the sides, typical of *macrophthalmus* (Wildekamp, 1995).

The present material also shares derived characteristics with another group of two related and relict species, named *Congopanchax* from the mid-Congo basin (Huber, 1998a):

- a tubular supraorbital system with 2 pores (and not 3, like in *Poropanchax*);
- a uniform green-blue shining color on male sides;
- the posterior shape of the caudal fin, without acuminate corners;
- a longer extension of ventral fins in filaments.

It is distinctive from *Congopanchax* by the very backward insertion of the dorsal fin (D/A= +8 or 9, versus +3 or 4), by the lack of a bilobate dorsal and anal, and by a small, but not dwarf size.

Wildekamp (1995), while forwarding the open supraorbital system of his Nigerian material of *scheeli*, establishes that the system of 2 pores of *Congopanchax* is variable and that juveniles indeed show 3 pores like *macrophthalmus*, the middle pore being closed at some stage.

This situation pushes us to hypothesize that all these fishes belong to a monophyletic line of evolution, with a disjunct distribution, near and on the coast and inland in the Congo basin. It is possible that future collections establish the presence of components of this line in the lower Congo basin, making the bridge between the two distribution patterns available (Huber, 1998a). *Poropanchax* is a taxon of that group, *Congopanchax* being relatively more primitive according to external characters. This implies a migration route from the Congo cuvette, into the coastal plain of Gabon, then to Nigeria and further Northwest for the entire group (see further distribution).

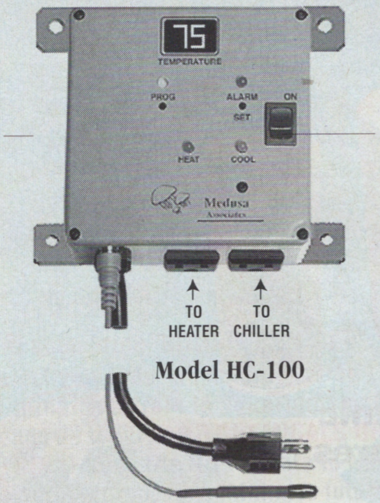
The full diagnostic characters of this monophyletic line of Cyprinodonts, which receives the generic name *Poropanchax* in a new sense, has been presented in a more global survey of the Aplocheilichthyins (Huber, 1998a), after the processing of the systematic software, P.A.U.P. 3.1, for 74 external characters.

Distribution, With General Comments On The Biogeography Of Brackish Oviparous Cyprinodonts:

With this report, the distribution of *Porop. scheeli* is extended to N.W. Gabon (map 1).

It is likely that it also lives in the available lagoons of S.W. Gabon, and why not in Congo to Angola, like its ecological counterpart, *Aplocheilichthys spilauchen*? Both are often found sympatrically, as in Nigeria and on the Island of Bioko, off Cameroun. Alternatively, no report is available for *scheeli* west of the Lagos area in Nigeria, but this needs further studies, since some uncontrolled reports of *normani* or *rancureli* in brackish waters may be erroneous (map 1).

On the other hand, *Aply. spilauchen* inhabits the same niche from the

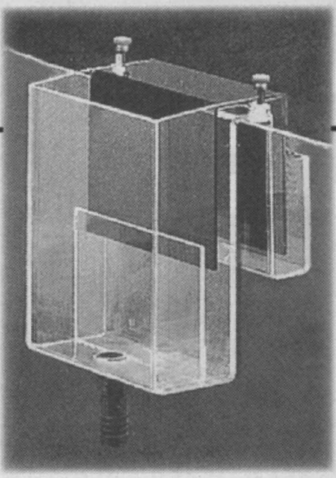


Sénégal River to Angola, near Luanda, but it is more opportunistic since it lives more inland, e.g. at Lambaréné in Gabon, some 150 km upstream in the Ogooué River Delta in the Atlantic Ocean.

Specialized species dwelling in brackish to marine habitats are numerous in oviparous (and viviparous!) Cyprinodonts. Not a single coast of the general distribution (maybe with the possible exception of some parts of the Pacific Ocean coast or the Sahelian desertic Atlantic coast, North of Sénégal) is not occupied.

Here is a comprehensive list of the concerned species:

- *Aply. spilauchen* and *Porop. scheeli*, in Western Atlantic Africa.
- *Pantanodon stuhlmanni* (*podoxys* is a junior synonym, according to Seegers, 1996) and *P. madagascariensis* in Eastern Indian Africa: the former in Kenya, Tanzania and the latter in Madagascar. The Aplocheilichthyin species, named *myaposae* in Southeastern Africa; maybe also in Southwestern Africa, at least according to Poll (1967) in Angola (or a related species). *Aphanius dispar* from Somalia to Western India. Without forgetting the non restricted to brackish biotopes but rather opportunistic freshwater species of the genus *Pachypanchax* (suggested for *nuchimaculatus*) in Madagascar and (demonstrated for *playfairii*, at least during high sea levels during the Cenozoic) in the Seychelles.
- *Rivulus marmoratus* and the related *Riv. caudomarginatus*, more opportunistic and primitive, in Eastern Atlantic America, from Florida in the USA to Southeastern Brazil and perhaps Argentina. *Cyprinodon variegatus* and its numerous subspecies from Cape Cod in Northwestern U.S.A. to (British) Guiana. The species of the relict genera *Floridichthys, Adinia, Jordanella* and *Garmanella* from Florida to the Yucatan peninsula. The various often sympatric *Fundulus* species *(heteroclitus et al., majalis et al., jenkinsi* and *luciae*) and *Lucania parva* from Canada to, for some of them, Yucatan and Belize.
- *Oxyzygonectes dovii* in Pacific Western America from Costa Rica to



Panama, at least. *Fundulus parvipinnis* from California (U.S.A.) to Baja California (Mexico).

- *Aphanius fasciatus*, all over the Mediterranean mainland and island coasts.

In ecological terms, all these species are not, however, identical: most show a decided but not exclusive preference for specific subniches and a variable tolerance to salt contents, as brackish biotopes are extremely variable in static and dynamic definitions (e.g., river-dominated, tide-dominated, wave-dominated mangroves in Robertson and Alongi, 1993). For example:

- some live extensively in seawater, near the coast or farther off-shore in shallow waters near reefs (*Riv. marmoratus, Aphanius fasciatus, F. parvipinnis, Cyp. dearborni*);
- some swim upstream to estuaries or small coastal rivers during their life cycle into freshwaters, like for breeding (*Luc. parva*...);
- some are lagoon-restricted, with little invasion inland (*Porop. scheeli, P. stuhlmanni* and *P. madagascariensis, Oxy. dovii*);
- some are more opportunistic since they are collected as adult in both fresh and brackish waters, either from an inland, even hilly, basis (*Pachypanchax*), or from a more salted basis (*Aphanius dispar*, the *Fundulus* sp. of the Atlantic coast).

These differences -- unfortunately very little studied in depth, except for *marmoratus* -- do not change the fact that almost all possible reclusive niches near the coast are occupied by oviparous, often sympatric Cyprinodonts. They then exhibit large distribution (by Cyprinodont standards!) while competing with a lot of other Teleosts. This is all the more surprising in that they are found in isolated discontinuous populations over their range and that 98% of Cyprinodonts are strictly in freshwaters.

Then, three theoretically important biogeographical questions arise:

1) Are the extant brackish Cyprinodonts, intermediate species of marine ancestors on their way to terrestrial freshwater biotopes? Are these species relict, with or without a phylogenetic link to the neighboring inland fauna?

2) Are species living now on one coast phylogenetically related to the species living on the other coast, facing it?

3) What does explain the present large distribution of the brackish species and where does their origin stem, for each of them?

The answers, if any, are diverse and not general, as usual in biology.

The answers, if any, are funded on the combination of our present knowledge of these fishes' phylogeny/biology and of the continents' drift, as a consequence of the plate tectonics from the global single Pangean continent about 200 million year ago (MYA).

It is presently supposed with solid argumentation in biogeography and geology that the complete detachment of Madagascar and India from Antarctica or Eastern Africa has not occurred before the late Jurassic (circa 150-135 MYA), that the separation of Africa and South America was started not before the early Cretaceous (circa 135 MYA) and completed much later (circa 90 MYA) and that the disconnection of North America and Eurasia was not irreversible before the Eocene (circa 50 MYA).

Parenti (1981) has argued -- and we concur, with the following considerations -- that the Cyprinodont ancestor(s) were already available in Pangea well before these major events. First, similar and primitive species of all groups and subgroups are known from various parts of the past Pangea and especially from its periphery. For example, it has been shown recently by DNA-studies that the Indo-madagascarian block *Pachypanchax-Aplocheilus* was basic to all other Aplocheilids, from both the old and the new world (Murphy & Collier, 1997). For example, it has also been shown by DNA-studies that the Mediterranean genus *Aphanius* shares the same Cyprinodontin ancestor with the geographically distant Andean genus *Orestias* and to a lesser extent with the North American genera allied to *Cyprinodon* (Parker & Kornfield, 1995). For example, it has been also established by DNA-studies that the neotropical genus *Fluviphylax* from mid-Amazonia is related to both West and East African Aplocheilichthyins (Meyer and Lydeard, 1993). In addition, all these findings have been corroborated by osteological and morphological studies (e.g., Costa, 1996; 1997 in addition to Parenti).

Second, fossils of the extant Northern genera have been discovered from Pliocene, lower Miocene (i.e., not more than 20 MYA) in South America, North America, and Europe from France/Germany to Czechoslovakia (i.e., well inland on those continents). This corresponds to their minimum age: their actual age could be much older.

Many of them show similar characters to the extant species and were placed by paleontologists in the same genera than extant species. This, hypothetically, means that the past recent distribution of Cyprinodonts was much larger than today, that fossils of present major phenotypes were available inland after the major continental divisions, and that the origin of today's brackish species is definitely to be found inland, and not in the sea, which has been abandoned by Cyprinodonts' ancestors for a very long time. Theoretically, our reasoning concerning today's brackish species could be different whether they are living at the periphery of the past Pangea or somewhere along a Pangea divide. In fact, we shall see hereafter that the direct ancestors of today's brackish species are all coming from the neighboring coastal regions.

Species living today at the periphery of the past Pangean continent, such as *Oxy. dovii, F. parvipinnis, Pachypanchax* sp., *Pantanodon* sp., are not much concerned by the phylogenetic aspects of the plate tectonics. Obviously, they have no close link with the species of the other side of Pangea (the contrary would mean that their ancestors would be sea fishes primarily). Actually, they have invaded their present territories vicariously through flooded land or along the coastal shallow sea waters. All, but one, have today a closely related counterpart in “neighboring” freshwaters.

The single exception is *Oxy. dovii* which is completely isolated, strongly primitive and distinctive from its distant relatives of the viviparous genera *Anableps* and *Jenynsia* from Atlantic South America. A considerable extinction must have taken place in the in-between regions, the gap being filled by other species, including maybe *Rivulus marmoratus*, in part.

For example, *F. parvipinnis* is related to *F. lima* from nearby freshwater springs and to the fossil *F. lariversi* from Nevada, but not the other Atlantic species of *Fundulus* (Bernardi & Powers, 1995).

Another example is the *Pachypanchax* sp. from Madagascar and the Seychelles have no counterpart in East Africa (except as transplanted by man!), but the once neighboring *Aplocheilus* from India are related to them.

The last example, are the two toothless *Pantanodon* sp. which are not known from the coasts, along the channel between Africa and Western Madagascar, and their specialized filtering capacity is not shared by any other Cyprinodont. They are related to inland Aplocheilichthyins (maybe *Hypsopanchax*, hypothetically in Huber, 1998a).

In total, one must admit -- or better hypothesize -- that these peripheral brackish species which all exhibit rather primitive and/or specialized characters in their groups are recluded in their biotope and isolated in their distribution since long ago. They have lost the possibility of gene exchanges with neighboring relatives from the coastal plain.

They can be regarded as relict, since their distribution is not much extended (by no means, like the post-divide species) and since no highland counterpart of them is reported.

Species living today on the coasts of the continental divide, i.e., on both sides of the Atlantic Ocean, might well be related to each other. However, not surprisingly, they are not! Each is linked with nearby inland species, but not with a pre-divide stemmed species. This means that their present distribution is the result of post-divide opportunism: no pre-divide already brackish ancestor has split and established itself to give birth to today's descendants in the very similar biotopes of estuaries and lagoons on both sides of the Atlantic, even if these mangronian biotopes may have been available as early as the drifts (90-120 MYA)! For example, *Aply. spilauchen* and *Porop. scheeli*, both Aplocheilichthyins, are facing *Riv. marmoratus* and *Riv. caudomarginatus*, both Rivulins: they have nothing in common except being Cyprinodonts. The Aplocheilichthyins have only one distant relative in America: the strictly freshwater genus *Fluviphylax*, from the mid Amazon and Orinoco drainages; but their closest relatives live in Africa, not far inland, with a parallel distribution (*Porop. macrophthalmus et al., Congopanchax* sp. for *scheeli*; see supra). The Rivulins have many distant relatives in Africa, belonging to *Aphyosemion s.l.*, but none of them is a brackish water dweller; their closest relatives in the freshwater genus *Rivulus* are not known, maybe other primitive species like *Riv. cylindraceus* (Huber, 1998b). For example, the Fundulins (*Fundulus* sp. *et al.*) and the Cyprinodontins (*Cyprinodon* sp. *et al.*) from Northeastern America do not face any Cyprinodont in Northwestern Africa from Sénégal to Tanger and in Southwestern Europe from Gibraltar to Western France; their relatives (*Valencia* sp.; *Aphanius* sp.; respectively) are densely living along the Mediterranean coasts and inland, but not West of the Gibraltar detroit. One could argue that their putative counterparts in Western Atlantic Africa have suffered extinction during the recent glacial, desertic periods, but this would also concern the nearby Mediterranean species and fossils might have been discovered near the present coasts.

Indeed, this situation leads us to hypothesize that the present coastal and marine distribution of *Aph. fasciatus* in the Mediterranean coast and of *Aph. dispar* in the Red Sea, the Persic Gulf and the Indian Ocean is a result of a less old invasion, posterior to the closure of the Mediterranean sea and the collision of Africa with Euro-Asia (circa 15 MYA). If this is true, then it would be a marvelous coincidence and a "retour aux sources" since the first Cyprinodont ancestor is thought to have originated from the Tethys Sea (a paleo-primitive sea, lying east of Pangea), with a minimum age of 150 MYA (late Triassic, Parenti, 1981 and earlier authors).

The third, and last, question regarding the present distribution and the center of origin of the present brackish Cyprinodonts is exciting but has only hypothesized established answers, as yet. For example, why *Rivulus marmoratus* has managed to invest more than 5000 kilometers of coasts? And from where does it stem, the Caribbeans or Uruguay-Argentina or somewhere in-between, say in Venezuela Guyanas (like it is hypothesized for other *Rivulus* species) (Huber, 1998b) before spreading North and South? Both extreme hypothesis could also be acceptable: in the Northern distribution, i.e., the Caribbeans, two very primitive species of *Rivulus* are encountered, *Riv. cylindraceus* and *Riv. roloffi*, having migrated from South America (Murphy & Collier, 1996); in the Southern distribution, from Rio de Janeiro to Santos, a close relative, also brackish, *Riv. caudomarginatus*, is living sympatrically with even more morphologically primitive characters (higher LL counts, deeper body, not hermaphroditic).

For example, and to go back to the main subject, *Porop. scheeli* (and conversely, *Aply. spilauchen*?) has managed to invest at least 2000 km of coast (resp. 4500 km). Morphological characters (*Congopanchax* exhibits more primitive features) support a link with the Congo fauna, not with the Sénégal River.

Regarding the present distributions, two models may be proposed to explain the huge discontinuous range of isolated populations for all extant brackish species linked with the Pangean divide: dispersal through coastal sea with the maintenance, even now, of a homogeneous genetic pool; or vicariance along the coast when suitable -- mainly mangrovian -- biotopes were continuously available. Currently, there is no answer but, hopefully, they will come from DNA molecular studies.

Differences at both ends of the distribution in color pattern for *Riv. marmoratus* (including *caudomarginatus*) and in micromorphological characters as we have seen in our angelfish, *Porop. scheeli*, are clues for the second scenario with a southern origin (Huber, MS). Mangroves are not alike all over the world, especially in tropical regions, and the four extant genera need muddy swamps over salinic soil and warm seas which explain their present discontinuous distribution. Some plant lineages are very old, possibly just arising after the first Angiosperms, along the split of Pangea (Huber, MS). Above all, it is to be emphasized that the present climatic conditions are very different from the past. During the Holocene, especially during the Last Glacial Maximum (circa 18,000 years ago) (Huber, MS), the level of the Atlantic Ocean had decreased by about 120 m and the coast had expanded by about 40 km and mangroves were scattered and, reciprocally, during wet peaks (e.g., the Holocene Climatic Optimum, circa 8500 years ago). These conditions and the associated fluctuations must have completely revolutionized the biotopes of our brackish species and their continuity (exemplified by the known fossil mangroves) all along the distribution. Besides, older warmer and wetter periods (e.g., the Miocene Climatic optimum 15-17 MYA) corresponded to much higher sea levels and a strong expansion of mangroves and brackish lagoons, with continuous distributions and opportunity of strong expansion for the brackish Cyprinodonts (Huber, MS). Times used to be much better than today, for our brackish Cyprinodonts!

Acknowledgements:

Prior to its submission, the manuscript has strongly benefited from the kind advices of J. Daget (Paris), R.H. Wildekamp (Gemert, Holland) and R. Castelo (Bioko Island, Equatorial Guinea) and also of *C. sastre* (Laboratoire de Phanérogamie, MNHN Paris) regarding mangroves. They are warmly thanked, together with the reviewers and FAMA editorial staff. Also, the aquarist collector, H.M. Auguste for his patient observations in the field and in the aquarium, and for granting us with live and preserved specimens. A special thought is addressed to Glen E. Collier (Tulsa, Oklahoma USA) who raised our interest in plate tectonics and phylogenetic relationships, through his works (*op. cit.*) with Bill Murphy, associating biogeography and molecular DNA experiments and who so kindly cooperated with us on *Aphyosemion* genetic items.

Dedication:

This study is dedicated to Dr *h.c.* Joergen J. Scheel who left us in the fall 1989, nearly a decade ago: he has brought so much to the initial modern knowledge of his African "Rivulins" and of Aplocheilichthyins to our generation, including ourselves by direct mastering. Despite the fact that he described few new species (21), his works (notably 1968, 1974) were acknowledged by the naming of three distinctive species after him: along with *Porop. scheeli*, *Aphyosemion scheeli* Radda, 1970 and *Aphyosemion joergenscheeli* Huber & Radda, 1977. There is no doubt that he would be passionately interested by the variation in the frontal neuromast pattern of *Porop. scheeli* and more importantly as a genetician and as a systematist by the revolution brought by DNA studies and by computer programs (like PAUP) in phylogenetic systematics during the last ten years.

Paris, December 1997.

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Post-finalization note: the mention "Huber, MS" corresponds to an important in-between published booklet (available against the value of 60 french francs in int'l post-office coupons from the author): **Huber, J.H. 1998.** Comparison of Old World and New World Tropical Cyprinodonts. A parallel outlook of similar and distinctive characteristics regarding distribution, evolution, ecology, morphomeristics, genetics, behavior and color pattern. *Société française d'Ichtyologie* Ed.: 109 pp., 17 Figs.